Submersion Tolerance of some Diplopod Species

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ABSTRACT

Submersion tolerance of *Polydesmus denticulatus* was compared to that of other diplopod species. About ten specimens of five species were placed individually in plastic tubes and flooded in an aquarium with aerated water (temperature 9±1°C). The highest median tolerance times were found in *Polydesmus denticulatus*, but one specimen of *Brachyiulus bagnalli* even reached a higher maximum of 65 days submersion. The other species are considerably less tolerant. In the four julid species median submersion tolerance times are significantly correlated with the surface/volume-ratio. *Polydesmus denticulatus*, however, is an outlier, and shows comparably higher tolerance values. The possible mechanisms of submersion tolerance are discussed.

RÉSUMÉ

Tolérance à l'immersion chez quelques espèces de diplopodes.

La tolérance à l'immersion de *Polydesmus denticulatus* a été comparée à celle d'autres espèces de diplopodes. Une dizaine de spécimens de cinq espèces ont été placés individuellement dans des tubes de matière plastique et immergés dans un aquarium contenant de l'eau aérée (température 9±1°C). En moyenne, la plus longue durée de tolérance à ce milieu est présentée par *Polydesmus denticulatus*. Cependant un invidu de *Brachyiulus bagnalli* a atteint la durée maximale de 65 jours d'immersion. Les autres espèces sont nettement moins tolérantes. Chez les quatre espèces de julides, la durée de tolérance à l'immersion est corrélée de manière significative avec le rapport surface/volume. Toutefois, *Polydesmus denticulatus* reste un cas particulier, montrant une tolérance à la submersion plus élevée. Les mécanismes éventuels de cette capacité sont discutés.

INTRODUCTION

Diplopods are usually supposed to be weak tolerators if they become submerged by rain or inundation (BLOWER, 1955; EISENBEIS & WICHARD, 1985). However, HOFFMAN (1978) reports a diplopod from Papuan caves entering voluntarily the water, ADIS (1986) describes long term submergence in an Amazonian diplopod, and in an investigation of floodplain soil animals the widespread European diplopod *Polydesmus denticulatus* was shown to survive up to 75 days in oxygenated cold water (ZULKA, 1991, 1992).

The present experiment should decide if this is a special adaptation of *Polydesmus denticulatus* to life in flood plains or if diplopods in general are able to withstand submersion longer than previously expected.

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MATERIAL AND METHODS

Specimens of *Polydesmus denticulatus* C. L. Koch, *Brachyiulus bagnalli* (Brölemann), *Ophyiulus pilosus* (Newport), *Cylindroiulus boleti* (C. L. Koch), and *Leptoiulus proximus* (Némec) were collected by hand in May 1992 in an alder forest near Marchegg, Lower Austria. All these species are widespread in Central Europe and inhabit a vast range of habitats (BLOWER, 1985), but *P. denticulatus* is the only one of them living also in temporarily flooded areas and surviving inundations submerged (ZULKA, 1991). Since the females of *Ophyiulus pilosus* and *Leptoiulus proximus* could not be separated from each other and from the syntopic *Julus scandinavius* with certainty, only males of these two species were used in the experiment. About ten specimens of each species were placed individually into plastic tubes of 2.2 cm diameter and 5.2 cm height that were closed with gauze. The tubes were flooded with aerated water of 9±1°C in a 12 litre-aquarium. Bubbles from an air stone connected to an aquarium pump maintained oxygen saturation in the water as well as slow continuous circulation of the water body. Air bubbles in the tubes trapped beneath the gauze cover were sucked off with a pipette. Oxygen saturation was measured with a WTW oxymeter at the beginning and near the end of the experiment and ranged between 94% and 98%, i. e. around 10.4 mg/l. Typically the animals adhered at the gauze cover. The tubes were checked daily and the animals were removed when their body became elongated (endosmosis) and they were unable to walk anymore.

To estimate the surface-volume ratio of the species, the julids were modelled as cylinders with a surface $S=2\pi r(r+h)$ and volume $V=\pi r^2h$, leading to a surface-volume ratio $R=2(r+h)/rh$ (r: radius, h: height). However, in *Polydesmus denticulatus* the cylinder model would have underestimated the surface-volume ratio because of the well-developed paranota. Thus, the calculation was based on a cross-section geometry as described in Figure 1 and leads to $S=2\pi r(r+h)+4rh$, $V=4r^2h$, $R=(\pi(r+h)+4rh)/2rh$. For r and h the average values were taken from SCHUBART (1934).

The medians of the submersion times were compared by Kruskal-Wallis ANOVA with subsequent multiple a-posteriori comparisons after CONOVER (1980), see also BORTZ *et al.* (1989), p. 231. The average ranks for every species were tested against:

$$\Delta\bar{R}_{(crit)} = t_{(N-k,\ \alpha/2)} \cdot \sqrt{\frac{N \cdot (N+1)}{12}} \cdot \sqrt{\frac{N-1-H_{emp}}{N-k}} \cdot \sqrt{\frac{1}{N_j}+\frac{1}{N_j'}}$$

RESULTS

Polydesmus denticulatus showed the highest median submersion times of all five species (Fig. 2). However, the difference of the medians between *P. denticulatus* and *B. bagnalli* is not significant (Table 1). The maximal tolerance time in *B. bagnalli* was even higher (Fig. 2) with one individual drowning only after 65 days. The other species are significantly less tolerant. The maximal of survival time in *Ophyiulus pilosus* and *Leptoiulus proximus* are about two weeks. Females generally showed a better performance (Fig. 3), but the differences between sexes were not significant.

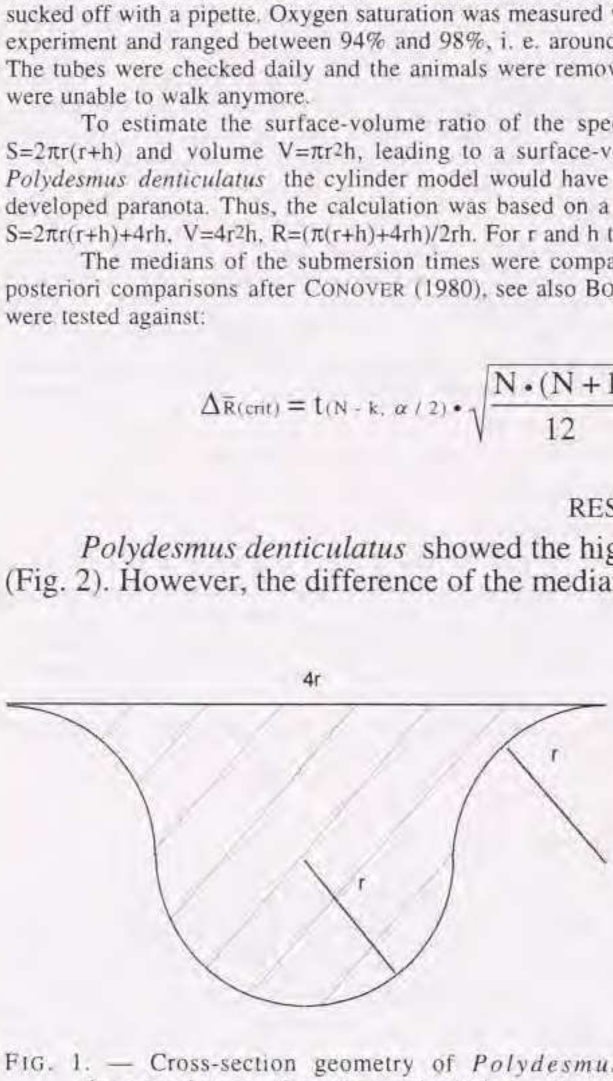

FIG. 1. — Cross-section geometry of *Polydesmus denticulatus* for the calculation of the surface/volume ratio $R=(\pi(r+h)+4rh)/2rh$.

In Figure 3 the median survival time is plotted against the surface-volume ratio R. The values are scattered around the regression line 1 and the correlation between survival time and R is insignificant ($r = 0.53$). However, if one excludes males and females of *Polydesmus denticulatus* as obvious outliers, the correlation becomes significant (regression line 2, $r = 0.88$, $P<0.05$, two-tailed). If one takes only males into consideration, the fit of the regression line gets even better and the correlation becomes highly significant (regression line 3, $r = 0.99$, $P<0,01$, two-tailed). This suggests, that in Julidae the survival times are to a high extent determined by the surface/volume ratio: the smaller the species, the higher the submersion tolerance.

TABLE 1. — Multiple *a-posteriori* contrasts after KRUSKAL-WALLIS-ANOVA between species (CONOVER, 1980). n. s. = not significant, * = significant (P<0.05).

	Polydesmus denticulatus	*Brachyiulus bagnalli*	*Cylindroiulus boleti*	*Ophyiulus pilosus*	*Leptoiulus proximus*
Polydesmus denticulatus		n.s.	*	*	*
Brachyiulus bagnalli	n.s.		*	*	*
Cylindroiulus boleti	*	*		*	n.s.
Ophyiulus pilosus	*	*	*		n.s.
Leptoiulus proximus	*	*	n.s.	n.s.	

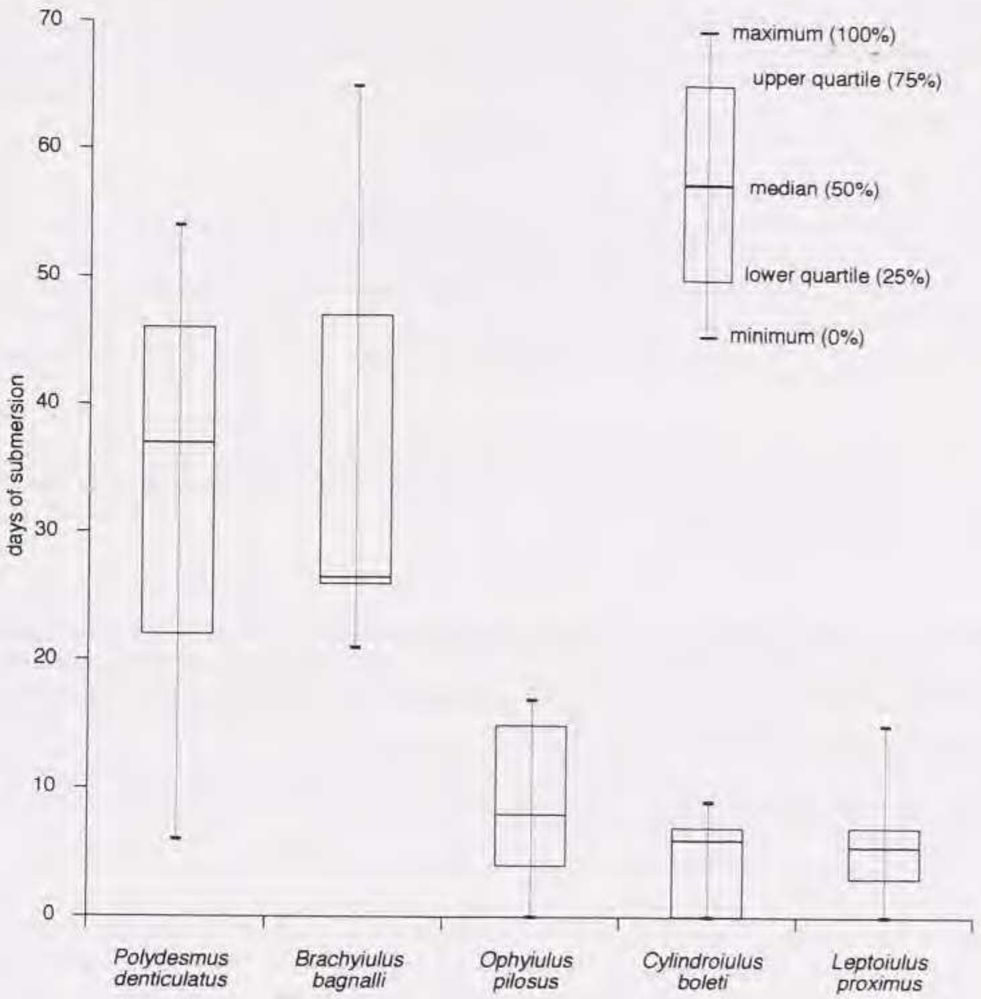

FIG. 2. — Survival times of five diplopod species submerged in water of 9±1°C and 94-98% oxygen saturation.

DISCUSSION

In *P. denticulatus* flooding tolerances are highest. But there are small julids like *B. bagnalli* with survival tolerances of the same magnitude that do not live in flood-prone habitats. So submersion tolerance of adults cannot be the only factor to explain why *P. denticulatus* can live in flooded places and others cannot. The unusual phenology of the species with reproduction in summer (SCHUBART, 1934) or the wide oscillations in population density indicating a high reproductive potential (BLOWER, 1970; ZULKA, 1991) may be additional preadaptations to life in floodplains.

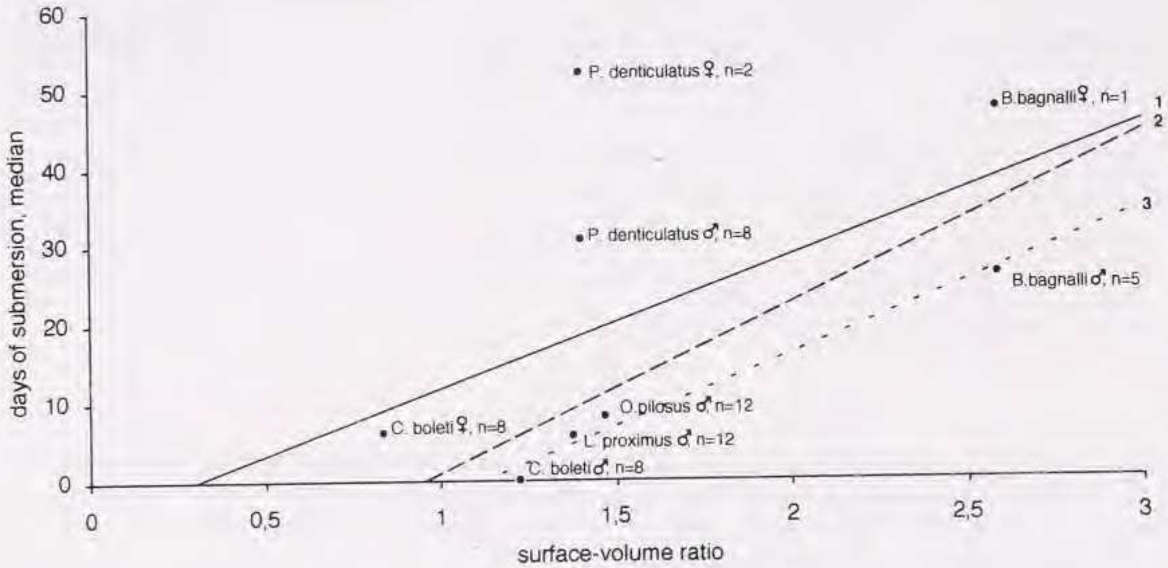

FIG. 3. — Scatter diagram of submersion tolerance times against surface/volume ratio in 5 diplopod species. 1: regression line based on all species and sexes, 2: regression line without *Polydesmus* data, 3: regression line without *Polydesmus* and female data.

In the other investigated julids flooding tolerances differ widely, depending mainly on the size of the species. Since most of them withstand a few days in water, they should be able to survive short time flooding caused by rain but unable to live in frequently inundated places.

Regarding the physiological mechanisms that allow the species a long survival under water, three possibilities could be imagined:

1. The species lives on its anaerobic pathways, and accumulates end products of glycolysis (see survey in CRAWFORD, 1978).

2. Oxygen supply by diffusion over the whole or over parts of the body cuticle is sufficient.

3. There are surface structures that maintain an air cover acting as a plastron. Such structures were found in the tropical millipede *Gonographis adisi* (MESSNER & ADIS, 1988).

In the present experiment the first possibility cannot be excluded, but it is rather unlikely, since the tolerance times are long and *Polydesmus denticulatus* drowns soon when submerged in unsaturated water (ZULKA, 1991).

There are indications for the second possibility at least in julids, since tolerances are highly correlated with surface/volume ratio.

No continuous air film around the body was observed except for the very first time when the animals got under water. When the last air bubbles between the hind edges of the metazonite and the ring duplicatures had already disappeared for a long time they still were active. However, spiracle structures might act as an interface between water and tracheal air, preventing the tracheae from being flooded and enabling plastron respiration. In this case, a similar relationship between tolerances and surface/volume ratio should be expected, since the spiracle area is correlated with the body surface.

Possibly the main oxygen source in all species is cutaneous diffusion, but in *P. denticulatus* special features like spiracle plastron structures (MESSNER, *in litt.*) could enhance the air supply under water. This would explain the higher tolerance values in this species (Fig. 3).

From the present data a clear decision is not possible. A comparison of flooding tolerances among *Polydesmus* species covering a broad range of size classes and living in very different habitat types in the East Alps (TADLER & THALER, 1993) should further elucidate the problem.

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